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SOME FACTOR RELATIONS IN MAIZE WITH REFERENCE TO LINKAGE

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IN view of the many distinct Mendelizing characters known in maize (*Zea mays* L.) it has been rather surprising that so few cases of linkage have been reported in this plant up to the present time. The number of chromosome pairs, about ten, is not large for plants and about twenty distinct contrasting factors are known of which the inheritance can be easily followed and about as many more which offer some difficulty in following in transmission but which can be used more or less satisfactorily in carrying on experiments on linkage. The writers have made no systematic search for cases of linkage in maize, but having found, almost accidentally, what seems to be a fairly good case of linkage between the tunicate factor which determines the production or inhibition of the glumes covering the seeds and the factor for starchy or sweet endosperm, the results are reported here in the hope that they may be of use to others who may be pursuing investigations along this line.

Collins and Kempton (1911) were the first to record a case of linkage in maize. Their results involved the relation of endosperm texture, as contrasted in our ordinary starchy varieties with the waxy condition found in Chinese varieties, to the color of the aleurone layer. They did not determine which of the several factors concerned with aleurone color was involved in this linkage. More recently Bregger (1918) has given additional proof of this case of linkage. He has determined the amount of crossing-over and has also shown that it is the C aleurone factor (East and Hayes, 1911; Emerson, 1918) which is the one involved. At about the same time Lindstrom (1917) reported the second case of linkage, that of one of

the factors of chlorophyll color G, with another aleurone color factor, this time the R factor, which in the presence of a suitable basic factorial combination produces red color in the aleurone cells. More recently Lindstrom (1918) has found another chlorophyll factor L linked with R and G. L is completely linked with R and both show about the same amount of breaks in the linkage with G. This makes the first group of three factors so far reported in maize.

LINKAGE BETWEEN TUNICATE EAR AND STARCHY-SWEET ENDOSPERM FACTORS

The curious type of maize, known generally in this country as pod corn (*Zea mays tunicata* Sturtevant) is considered by Collins (1917) not to be a pure type, but a heterozygous condition somewhat analogous to the blue Andalusian fowl. When selfed seed of the typical podded ears are planted Collins finds that three types of plants are produced: one type like the typical podded parent; one with normal ears without the enclosing glumes; and one anomalous type of a plant which does not produce seed in lateral inflorescences, but in perfect flowers in the tassels. On these last plants lateral inflorescences with much elongated glumes are produced, but are sterile. All these three types have been secured in about the ratio of 1:2:1 as expected on the assumption that a single Mendelian difference is involved and the heterozygote is distinguishable from both homozygotes.

Our own rather limited experience with this type of maize confirms Collins's conclusions. In 1915 seed of a typical podded ear was planted (there was no record whether it had been selfed or not). All three types which Collins described later were obtained. A number of typical podded plants were self-pollinated and grown the next year in the hope of getting a pure podded strain. At that time no thought was given to the possibility of its being a heterozygous type. The plants with seeds in the tassels were thought to be extreme variations from the

usual type. Nine selfed ears were obtained and grown the following year and all gave some plants with podless ears and others with seeds in the tassels as well as plants of the typical pod type. No record was made of the numbers in each class, but it was noted as rather surprising that all of the nine ears gave some normal non-pod plants.

An attempt was made to self-pollinate some of the plants with the peculiar terminal inflorescences which were easily recognized as the type which produced seed, but no seed was obtained where they were enclosed in a bag. Very little good pollen is produced in these tassels and probably all or most of the seeds which are produced on open-pollinated plants result from crossing with foreign pollen. One tassel with a number of such open-pollinated seeds was saved and the seed planted. No normal non-pod ears were obtained. Most of the ears were of the typical pod type or half-tunicate as named by Collins. All of these results bear out the assumption of Collins that the podded maize considered by Sturtevant (1899) as a separate species and stated by him to have been known for 300 years is not a constant type and has little more claim to specific rank than the blue Andalusian fowl.

One of the half-tunicate ears produced from the open-pollinated seed of the perfect flowered segregate was self-pollinated, and when examined this ear was found to have segregated into starchy and sweet seeds, showing that the plant which had furnished the pollen had sweet seeds. Since all the podded maize which had been grown up to that time was starchy and all of the sweet maize was non-podded, the cross involved the tunicate character and starchy endosperm from the female parent, and non-tunicate, sweet endosperm from the male. The starchy and sweet seeds were planted separately. There were 173 of the starchy and forty-three of the sweet seeds. Not a perfect 3:1 ratio, but reasonably close. All of the seeds were planted, but since not all of each type produced a mature plant, it is legitimate to correct the observed re-

sults according to the theoretical starchy-sweet ratio. The results obtained and corrected in this way are as follows:

	Starchy Tunicate	Starchy Non-tunicate	Sweet Tunicate	Sweet Non-tunicate
Found.	113	4	7	25
Corrected.	108.0	3.8	8.2	29.1
Starchy-sweet ratio				
Expected.	105.8	6.0	6.0	31.3
11:1:1:11 gametic ratio				

The numbers are small, but the distribution obtained is clearly different from a 9:3:3:1 ratio. The agreement with the nearest theoretical results, assuming linkage, is close ($P=.615$). The per cent. of crossing-over, 8.3, indicated by these figures is low. In the other cases of linkage reported, the percentages of crossing-over were much higher, 25.7 per cent. in the waxy endosperm-aleurone color combinations and 20 per cent. in the aleurone color-chlorophyll color combination with the exception of the one case where complete linkage has so far been found.

In making the classification all of the plants which showed the tunicate character, whether of the half-tunicate or full-tunicate type, were classed as tunicate, as contrasted to the normal plants. Segregation was clear between these two classes and there was little possibility of confusion even when the ears were immature. On the other hand, it was not always easy to distinguish full-tunicate from half-tunicate plants, as the tassels of the former class do not always produce seed, and the ears, which are quite characteristic when fully developed, are not so distinct when immature, and many of these plants were late in maturing. Any error of classification here does not affect the linkage results, however. There is one source of error in that the plants suckered profusely; many of these bore ears and tassels and were difficult to distinguish from the main stalk. The plants were grown in hills, and when classifying them it was not always pos-

sible to tell which was plant and which was sucker, so that the same plants may have been included in the count more than once.

The figures for the segregation with respect to the tunicate character together with the figures from a similar ear, which instead of segregating starchy and sweet segregated for yellow and white endosperm, are given as follows:

	Normal	Half-tunicate	Full-tunicate
Ear 1 { Sweet	25	6	1
Starchy	4	70	43
Ear 2 { White	10	19	14
Yellow	36	58	29
Found	75	153	87
Expected	79	158	79
1:2:1 ratio			

With regard to this second ear, which was similar to the first except that it was crossed with yellow, starchy, non-tunicate instead of white, sweet maize, it is to be noted that there is no indication of linkage between the factors for tunicate ear and yellow endosperm. The figures obtained compared to the expectancy are given herewith:

	Yellow Tunicate	Yellow Non-tunicate	White Tunicate	White Non-tunicate
Found	87	36	33	10
Corrected	88.1	36.4	31.9	9.7
Yellow-white ratio				
Expected	93.4	31.1	31.1	10.4
9:3:3:1 ratio				
P = .739				

EVIDENCE FOR LINKAGE BETWEEN ALEURONE COLOR FACTORS

Another case of linkage is suggested by the results of East and Hayes (1911) in the inheritance of aleurone color. From crosses of colorless aleurone by purple they obtained marked deviations from the expected ratios which they could not account for. At that time the first

cases of gametic coupling had just been published by Bateson and Punnett and the subject of linkage was not well understood nor its true significance realized. These writers considered the possibility of gametic coupling as a disturbing factor, but came to the conclusion that this phenomenon could not be concerned in their aberrant results.

One of the crosses studied involved two aleurone factors, the basic color factor C and the factor P (Emerson's Pr factor), with R present coming from both parents. This cross was expected to give a ratio of 9 purples : 3 red : 4 non-colored, but actually showed a large excess of purples and deficiency of reds. East and Hayes considered the possibility of linkage between the P and R factors, but since R, according to their theory, was homozygous, crossing-over between these two factors would make no visible difference in the F_2 results. On the other hand, since PC entered the cross from one side and pc from the other, the cross-over class pC, if there is linkage, would be red because of the presence of R. Hence any possibility of linkage should be looked for between the P and C factors. Such a situation would account for an excess of purples and a deficiency of reds in the cross under consideration. Another cross involving, in addition to the P and C factors, a color inhibiting factor likewise showed an excess of purples and a deficiency of reds.

Since it is always rather difficult to prove linkage from F_2 distributions alone, in this case it would be even more difficult because only one of the cross-over classes, if such it is, can be distinguished. The data of East and Hayes, as far as numbers go, do not agree with expectation from linkage with any amount of crossing-over, and since other crosses involving the same factors have been reported which seem to show independence, it is doubtful whether or not linkage really exists in respect to these two factors. It is more probable that the deviations from theory are to be looked for in either incomplete analysis of the factor relations or faulty classification of the seeds. Red seeds

graduate somewhat into purple and there may be a tendency to include reds among purples. If this were the case, however, wrongly classified purple seeds should sometimes give all red progeny or red and white progeny in the next generation. East and Hayes found no cases of this kind. The possibility of linkage between the P and C factors should be kept in mind until this point can be definitely settled.

OTHER FACTORIAL RELATIONS

Looking over East and Hayes's data for other cases of linkage or independence of factors there seems to be good evidence that the C aleurone and R aleurone factors are not linked, and also that the factor for sweet endosperm is not linked with either the R or P aleurone factors. In a factorial analysis of the characters of an organism with reference to linkage it is just as important to know the cases where no linkage is shown as those cases where it is shown. Collins and Kempton (1913) give data which indicate independence between sweet and waxy endosperm factors and in another paper (1917) independence between the *tunicata* and *ramosa* factors. East (1910) gives data which indicate that the two factors for yellow endosperm color are not linked with each other and it is quite probable that both of them are independent of the factor for sweet endosperm.

With this evidence we can attempt a beginning at an analysis of the factorial relations in maize. Three independent groups of factors can be tentatively proposed as follows:

Group I	Group II	Group III
Ww Endosperm Cc Aleurone Pp Aleurone (?)	Gg Chlorophyll Ll Chlorophyll Rr Aleurone	Ss Endosperm Tt Tunicate

The fact of no linkage between the Cc aleurone and the Rr aleurone color factors separates groups I and II. No linkage between Ww and Ss endosperm factors separates

groups I and III. No linkage between the Ss endosperm and Rr aleurone factors separate groups II and III.

Since the number of known factor differences in maize is already some three or four times the number of chromosomes, more definite knowledge of the behavior of all these factors in relation to each other will be awaited with interest. Especially since maize is one of the best materials from the plant side to which the chromosome hypothesis, as worked out in *Drosophila*, can look for contradiction or support.

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